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Validation of annulus formation in otoliths of largemouth bass *Micropterus salmoides* outside their native range

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Summary

The periodicity of growth zone formation was validated for largemouth bass *Micropterus salmoides* using edge analysis (EA) and mark recapture of chemically-tagged wild fish (MRCT) to test the hypothesis that one opaque and hyaline zone was deposited annually in sagittal otoliths sampled from temperate South African *M. salmoides* populations. For 35 fish recaptured in the MRCT experiment, the relationship between the number of growth zones posterior to the chemical mark and the time at liberty (0.04–1.38 years) did not differ significantly from a 1 : 1 relationship (*t*-test, $t = 0.76$, d.f. = 2,33, $P = 0.45$). This result was supported by EA, where periodic logistic regression and a binomial model linked with a von Mises distribution for circular data demonstrated that the frequency of otoliths with opaque margins followed a unimodal distribution (maximum October–January). Both the timing of growth zone deposition (spring) and the annual rate were consistent with results from validation studies conducted globally in localities ranging from 45°N to 33°S, and indicate that the growth zone deposition rate is annual throughout the native and introduced range of this species.

Introduction

Largemouth bass *Micropterus salmoides* (Lacépède, 1802) are important sport fishes in their native North America (Quinn and Paukert, 2009) and have been introduced into South America, Europe, Asia and Africa to develop opportunities for angling (Robbins and MacCrimmon, 1974; Quinn and Paukert, 2009; Skelton and Weyl, 2011). *Micropterus salmoides* established successfully in a wide range of recipient habitats where their predation has had impacts on native fish and macroinvertebrate communities (Gratwicke and Marshall, 2001; Takamura, 2007; Weyl et al., 2010; Ellender et al., 2011). As a result the species is now listed as one of the 100 of the world's worst invasive alien species (Lowe et al., 2000) and understanding its biology in invaded environments is important not only for managing fisheries but also for comprehending the role of this alien invasive species in aquatic communities.

The accurate and precise estimation of age is an important component of fish biology because it forms the basis for understanding the rates at which fish grow, mature and die (Campana, 2001). In fishes, age is most commonly estimated by counting alternating opaque and hyaline growth zones on calcified structures such as scales and otoliths (Campana, 2001). Age estimates are available for many *M. salmoides* populations in their native North America (e.g. Maraldo and MacCrimmon, 1979; Beamesderfer and North, 1995; Maceina et al., 2007) but relatively few ageing studies have been conducted in their introduced range (Yodo and Kimura, 1996; Weyl and Hecht, 1999; Lorenzoni et al., 2002; Beamish et al., 2005; Britton and Harper, 2005; Schulz and Leal, 2005). This situation precludes broader analyses of proposed hypotheses such as the attempt to link rapid growth rates of *M. salmoides* in its introduced range to temperature (Helser and Lai, 2004; Neal and Noble, 2006; Britton et al., 2010). The reasons for the paucity in ageing studies on this globally important species are not clear but may be linked with the costly (in terms of time) but fundamental requirement for validating growth zone deposition rate prior to using growth zone counts directly as estimates of age (Beamish and McFarlane, 1983; Campana, 2001).

Validation is considered a fundamental requirement in ageing because the interplay of environmental (e.g. temperature), behavioural (e.g. feeding, spawning) and biological (calcium metabolism) factors controlling the deposition of growth zones (Gauldie and Nelson, 1990; Campana, 1999) can result in different growth zone deposition rates not only between species in the same locality but also between populations of the same species. In a large impoundment in South Africa for example, the growth zone deposition rate was annual for native cyprinids (Winker et al., 2010b; Ellender et al., 2012), but biannual for the non-native common carp *Cyprinus carpio* L. which differed from the annual deposition rate validated for *C. carpio* populations elsewhere (Winker et al., 2010a). Common methods of validation include the indirect method of edge analysis (EA) and direct methods such as the mark-recapture of chemically tagged wild fish (MRCT) (Campana, 2001).

Edge Analysis is based on the assumption that a growth increment is formed on a yearly cycle, and that the outermost increment state frequency (opaque zone present or absent) should form a yearly sinusoidal cycle when plotted against time (Campana, 2001). EA therefore requires a large sample of hard parts from fish that are ideally collected at monthly intervals. Chemically marking wild fish relies on injecting, immersing, or feeding fish with a fluorescing, calcium-binding chemical such as oxytetracycline hydrochloride (OTC) which is rapidly incorporated into calcified structures at the time of marking and forms a permanent fluorescing band (Campana, 1999). The fish is then released back into the wild and recaptured after some time at liberty. On examination of the calcified structure from the recaptured fish, a permanent mark is visible under ultraviolet light and the growth increments formed distal to this mark can be counted and compared to the time that the fish spent at liberty (Campana, 2001). Both processes are time consuming, preclude the rapid assessment of fish age and require fairly large sample sizes of fish. Possibly because of such constraints, ageing studies on introduced *M. salmoides* populations in Portugal (Godinho and Ferreira, 1993), Italy (Lorenzoni et al., 2002), Puerto Rico (Neal and Noble, 2002), and Spain (Rodriguez-Sánchez et al., 2009), have been undertaken without prior validation. While the assumption made in these studies that growth zone deposition rate is annual may be valid, there has never been a comprehensive regional assessment of the growth zone deposition rate for *M. salmoides*.

In this paper, we use EA and MRCT to test the hypothesis that one opaque and hyaline zone was deposited annually in sagittal otoliths of *M. salmoides* sampled from four temperate South African populations and compare our results with those of a comprehensive collection of literature to test the common assumption that growth zone deposition rate in *M. salmoides* otoliths is annual throughout its distribution range.

Materials and methods

Study site

Fish were sampled from four impoundments in the Eastern Cape Province of South Africa. The impoundments are located at altitudes ranging from 66 to 755 m above mean sea level (amsl) in the temperate Eastern Cape Province of South Africa. Daylight and mean monthly air temperatures range from 9.8 h and 8°C in winter to 14.2 h and 26°C in summer (South African Weather Service (SAWS), 2012). Growth zone deposition rate was estimated indirectly using edge analysis (EA) from fish sampled from two impoundments: Mankazana (33°09′49″S; 26°57′09″E, 35 ha; 66 m amsl) and Wriggleswade (32°35′35″S; 27°33′07″E, 1000 ha; 723 m amsl) and directly by mark-recapture of chemically-tagged fish (MRCT) in three impoundments: Wriggleswade, Dames (33°19′22″S; 26°35′25″E, 6 ha, 500 m amsl) and Howarth (33°24′53″S; 26°20′15″E, 5 ha, 403 m amsl).

Edge analysis

For EA a total of 332 fish (38–619 mm FL) were sampled from the Wriggleswade Impoundment and 288 fish (46–490 mm FL) sampled from the Mankazana Impoundment monthly from February 2011 to April 2012. Samples were either donated by anglers and/or obtained from direct sampling by angling and gill netting. Fish donated by anglers were already dead whereas fish from direct sampling were sacrificed by concussion and destruction of the brain. Each fish was then measured to the nearest millimetre fork length (FL), dissected to determine sex, and the sagittal otoliths removed for later analysis.

Sagittal otoliths were prepared according to Weyl and Hecht (1999). Otoliths were burnt over a low intensity ethanol flame until they turned light brown to enhance the visibility of growth zones, set in clear polyester casting resin and sectioned transversely through the nucleus using a double-bladed diamond edged saw to a thickness of 0.3 mm. Sections were then read under a binocular microscope using transmitted light at variable magnifications (10–40×). Growth zones were reflected as alternating opaque and hyaline zones (Fig. 1) and according to common practise one opaque/hyaline growth zone pair was considered a growth zone and counted. Optical appearance of the edge of the otolith (either opaque or hyaline) was also noted. To reduce potential reader bias each otolith was read three times with at least a 1-week interval between readings and with no

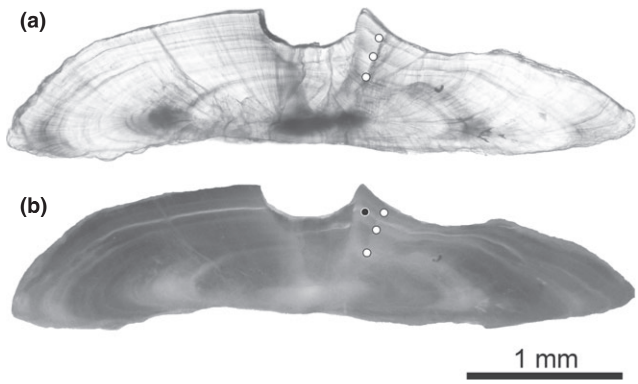

Fig. 1. A 3-year-old 240 mm FL *Micropterus salmoides* tagged with 60 mg kg^{-1} body mass oxytetracycline hydrochloride and released into Dames Impoundment on 10 December 2006 and recaptured on 15 April 2008. White circles (a) = annual opaque growth zones under reflected light; black circle (b) = fluorescent band of OTC under ultraviolet light deposited during tagging

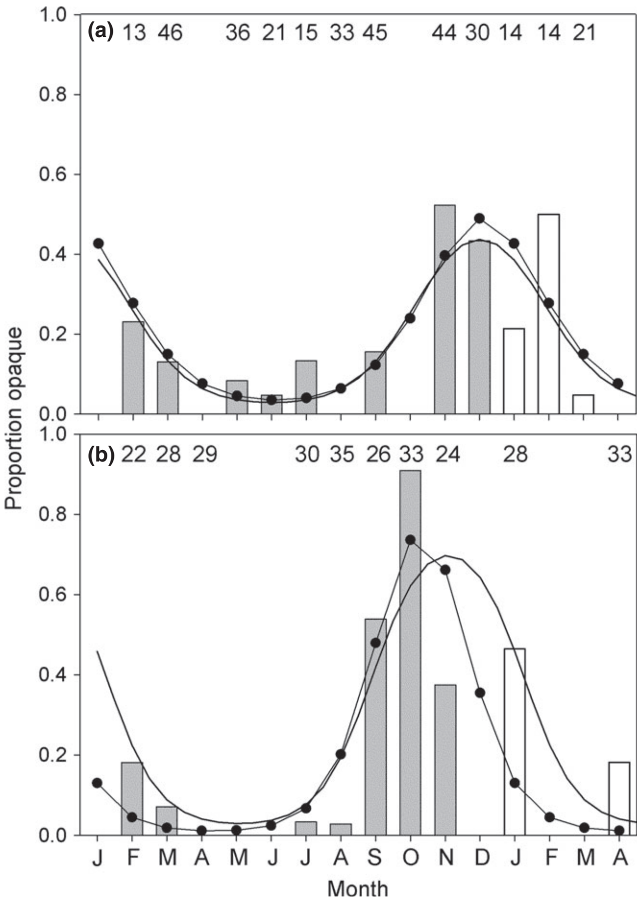

Fig. 2. Proportion of opaque sagittal otolith margins from *Micropterus salmoides* sampled monthly from Wriggleswade (a) and Mankazana (b) impoundments, January 2011–April 2012, Eastern Cape, South Africa. Solid line = predicted binomial periodic regression model; connected black dots = predicted annual von Mises distribution. Observed opaque proportions given as bars; grey bars = restricted year of data used for von Mises distribution analysis. Sample sizes per month given at the top of the bars

Table 1
Parameter estimates from logistic periodic analysis predicting temporal proportion of opaque zone deposition over a 1-year period for *Micropterus salmoides* in Wriggleswade and Mankazana impoundments, Eastern Cape, South Africa

Parameter	Wriggleswade			Mankazana		
	Full	Annual	Biannual	Full	Annual	Biannual
β_0	−1.23	−1.88	−1.47	−1.84	−1.33	−0.96
β_1	−1.39	0.01	−0.30	0.16	−1.00	−0.66
β_2	1.29	1.63	0.78	2.36	1.92	0.20
PE	16.15	12	6	10.18	12	6
d.f.	4	3	3	4	3	3
ln *L*	−145.32	−146.09	−160.50	−127.87	−129.57	−163.15

Periodicity (PE) was estimated for full models and fixed for unimodal and bimodal models

Table 2
Akaike Information Criterion characterising periodicity of growth zone formation as annual (lowest AIC values) for *Micropterus salmoides* populations, Wriggleswade and Mankazana impoundments, Eastern Cape, South Africa using both von Mises and wrapped Cauchy distributions

	AIC		
	No cycle	Annual	Biannual
Wriggleswade			
von Mises	289	250	277
Wrapped cauchy	289	248	276
Mankazana			
von Mises	266	181	231
Wrapped cauchy	266	163	236

reference between the otolith and the size of fish from which it was obtained.

For EA the optical appearance of the otolith edge was then categorised as opaque zone present (1) or absent (0) and modelled using two statistical methods. Firstly a periodic logistic regression (Flury and Levri, 1999) was carried out using the same procedure explained by Winker et al. (2010a) where the null hypotheses (H_1^0) that growth zone deposition is annual (PE = 12), and (H_2^0) that growth zone deposition is biannual (PE = 6) were tested. Secondly using the method recommended by Okamura and Semba (2009) in which a binomial model is linked with a von Mises distribution for circular data, using the Akaike Information Criterion (AIC) to determine if the periodicity of growth zones is categorised as no cycle, annual or biannual. The lowest AIC indicates the most supported periodicity category.

Mark-recapture of chemically tagged fish

Fish for MRCT were captured by angling, measured to the nearest mm FL, injected with 60 mg kg^{-1} fish mass of commercially available oxytetracycline hydrochloride (HiTet 120; Bayer, Leverkusen, Germany), tagged with either a Hallprint (Victor Harbour, South Australia) plastic dart (model PDL) or a T-bar anchor (model TBA-2) tag and released. Sample size depended on the environment. In Howarth Impoundment a total of 80 fish (200–480 mm FL) were marked between September and November 2004. In Dames Impoundment a total of 36 fish (200–500 mm FL) were marked during December 2006 and in Wriggleswade Impoundment 786 fish (213–582 mm FL) were marked and released between May 2011 and January 2012.

Upon recapture fish were sacrificed by concussion and destruction of the brain and sagittal otoliths were taken and stored in the dark to prevent the degrading effect of ultraviolet light on the fluorescence of the mark formed by OTC on calcified structures (Winker et al., 2010a). Otoliths were processed as described for EA with the exception that they were not burnt prior to processing. Sections were viewed under fluorescent (460–490 and 510–550 nm) light to determine the position of the fluorescent mark and under transmitted white light to count the number of opaque and hyaline growth zones distal to the fluorescent mark. Because one opaque and hyaline growth zone pair represents one growth increment, each was assigned a score of 0.5, such that the sum of the opaque (0.5) and hyaline (0.5) growth zones distal to the fluorescent mark could be plotted against time at liberty. A *t*-test was then used to test the hypothesis that the slope of the regression differed from a 1 : 1 relationship and the intercept differed from 0.

Results

Edge analysis

Observed and predicted data for both impoundments indicated that the highest proportion of otoliths had opaque margins from November to January (Fig. 2). Periodic regression parameters for samples from Wriggleswade and Mankazana impoundments are provided in Table 1. Periodic logistic regression analysis failed to reject the null hypothesis that one opaque zone was deposited annually in the Wriggleswade (χ^2 = 1.55, d.f. = 3, P = 0.21) and Mankazana impoundments (χ^2 = 3.40, d.f. = 3, P = 0.065) and rejected the alternative hypothesis that growth zone deposition was bimodal (χ^2 = 30.37, d.f. = 3, P < 0.05) (χ^2 = 70.57, d.f. = 3, P < 0.05) (Table 1, Fig. 2).

In addition, the method recommended by Okamura and Semba (2009) showed the lowest AIC values for an annual cycle in Wriggleswade and Mankazana impoundments compared to no cycle and to the binomial cycle (Table 2, Fig. 2).

Mark-recapture of chemically-tagged fish

Thirty-five chemically marked fish were recaptured after between 14 and 503 days (0.04–1.38 years) at liberty (Table 3). All otolith sections had a visible clear fluorescing band incorporated into them (Fig. 1). Those fish that were recaptured during or after the opaque zone deposition period predicted from EA had 2 to 14 growth zones prior to the mark and one growth zone (an opaque and a hyaline zone) distal to the fluorescent mark (Table 3). The slope of the

Table 3
Summary of *Micropterus salmoides* injected with oxytetracycline hydrochloride (OTC) and recaptured after being at liberty in the wild

Impoundment	Date injected year/month/day	Date re-captured year/month/day	Time at liberty (days)	FL_1 (mm)	FL_2 (mm)	ΔFL (mm)	Sex	Growth zones B	H	O	H	A	Edge	Age
Howarth	2004/11/19	2005/12/10	386	304	327	23	M	3	1	1	–	1	O	4
Dames	2006/12/10	2008/04/10	487	–	240	–	–	2	1	1	1	1.5	H	3.5
Dames	2006/12/10	2007/12/25	380	500	580	80	–	8	1	1	–	1	O	9
Dames	2006/12/20	2007/12/01	346	388	410	22	–	5	1	1	–	1	O	6
Wriggleswade	2011/05/14	2012/03/11	302	401	408	7	M	5	1	1	–	1	O	6
Wriggleswade	2011/05/14	2012/09/28	503	373	374	1	M	5	–	1	1	1	H	6
Wriggleswade	2011/05/15	2011/10/11	149	450	446	−4	F	9	–	1	–	0.5	O	9.5
Wriggleswade	2011/05/15	2012/03/11	301	388	404	16	F	5	1	–	–	0.5	H	5.5
Wriggleswade	2011/05/15	2011/10/11	149	430	430	0	M	9	1	–	–	0.5	H	9.5
Wriggleswade	2011/09/10	2012/03/11	183	355	342	−13	M	4	–	1	–	0.5	O	4.5
Wriggleswade	2011/10/08	2012/09/28	356	335	335	0	F	3	–	1	1	1	H	4
Wriggleswade	2011/10/08	2012/09/28	356	330	336	6	F	3	–	1	1	1	H	4
Wriggleswade	2011/10/08	2012/09/28	356	360	369	9	F	4	–	1	1	1	H	5
Wriggleswade	2011/10/08	2012/03/11	155	378	371	−7	M	6	–	1	–	0.5	O	6.5
Wriggleswade	2011/10/09	2012/09/28	355	410	451	41	F	7	–	1	1	1	H	8
Wriggleswade	2011/10/09	2012/09/27	354	357	358	1	F	3	1	1	–	1	O	4
Wriggleswade	2011/10/09	2012/03/11	154	425	422	−3	M	14	1	–	–	0.5	H	14.5
Wriggleswade	2011/11/19	2012/09/26	312	440	452	12	F	9	1	1	–	1	O	10
Wriggleswade	2011/11/19	2012/09/26	312	424	444	20	F	7	1	–	–	0.5	H	7.5
Wriggleswade	2011/11/19	2012/09/28	314	350	342	−8	F	5	–	1	–	0.5	O	5.5
Wriggleswade	2011/11/19	2012/09/27	313	348	349	1	F	3	–	1	–	0.5	O	3.5
Wriggleswade	2011/11/19	2012/09/26	312	385	370	−15	F	6	–	1	1	1	H	7
Wriggleswade	2011/11/19	2012/09/27	313	305	308	3	M	4	–	1	1	1	H	5
Wriggleswade	2011/11/19	2012/09/27	313	415	415	0	F	8	–	1	1	1	H	9
Wriggleswade	2011/11/20	2012/09/27	312	355	419	64	M	4	–	1	1	1	H	5
Wriggleswade	2011/11/20	2011/12/04	14	315	315	0	F	5	–	–	–	0	–	5
Wriggleswade	2011/12/03	2012/09/26	298	299	300	1	M	3	–	1	1	1	H	4
Wriggleswade	2011/12/04	2012/09/26	297	352	352	0	M	6	–	–	1	0.5	H	6.5
Wriggleswade	2011/12/04	2012/09/26	297	336	337	1	F	5	–	1	1	1	H	6
Wriggleswade	2011/12/04	2012/09/27	298	323	326	3	M	4	1	1	–	1	O	5
Wriggleswade	2012/01/14	2012/09/27	257	340	343	3	M	5	–	1		0.5	O	5.5
Wriggleswade	2012/01/14	2012/09/28	258	420	421	1	F	7	–	1	1	1	H	8
Wriggleswade	2012/01/14	2012/09/28	258	390	394	4	M	6	1	–	–	0.5	H	6.5
Wriggleswade	2012/01/15	2012/09/26	255	330	338	8	F	3	1	–	–	0.5	H	3.5
Wriggleswade	2011/09/10	2012/01/27	139	450	468	18	F	9	–	1	–	0.5	O	9.5

Summary includes the impoundment, number of opaque zones deposited before OTC injection (B), number of growth zones [O = opaque (0.5), H = hyaline (0.5)] deposited after OTC injection (A), and total number of growth zones (Age). Growth (ΔFL) in mm calculated as the difference between length at injection FL_1 mm and length at recapture FL_2 mm. Visual appearance of otolith edge as either opaque (O) or hyaline (H) also presented.

linear relationship between time at liberty (years) and the number of growth zones (linear regression, $F_{1,33}$, $r^2 = 0.61$, $P < 0.05$) was 0.89. The null hypothesis that the slope of the regression = 1 could not be rejected (*t*-test, $t = 0.76$, d. f. = 2,33, $P = 0.45$) and the intercept was not significantly different from zero (*t*-test, $t = 0.88$, d.f. = 2,33, $P = 0.38$) (Fig. 3). The present study was therefore able to validate the annual deposition of one opaque and one hyaline zone in adult *M. salmoides* aged between 2 and 14 years and from three different localities (Table 3).

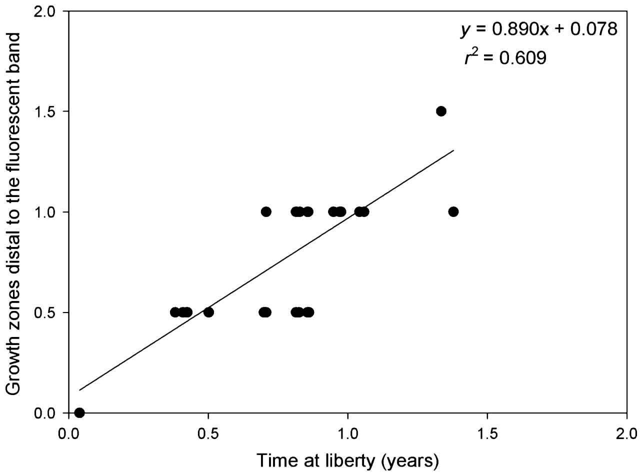

Fig. 3. Relationship between number of growth zones distal to the fluorescent band and time at liberty for *Micropterus salmoides* recaptured from Howarth, Dames and Wriggleswade impoundments, Eastern Cape, South Africa. Linear regression equation and r^2 value given

Discussion

This study confirmed the annual deposition of a single opaque/hyaline growth zone pair in four temperate *M. salmoides* populations in Africa using both EA and MRCT methods. While EA is considered a less robust validation method than MRCT because it is dependent on the reader recognising the state of the otolith edge (Campana, 2001), our MRCT results indicate that EA adequately validated the growth zone deposition rate in the Wriggleswade Impoundment where both methods were applied. These results are consistent with those recently undertaken on four South African cyprinids where EA and MRCT also provided complementary results (Winker et al., 2010a,b; Ellender et al., 2012), which supports the annual deposition found using EA, the most commonly applied method of validation in the literature (Table 4).

Table 4
Summary of studies on validation of *Micropterus salmoides* growth zone deposition rate in otoliths

Location	Coordinates	Method	Period	Max age
South Africa[1]	33°24′S, 26°20′E	EA, MRCT	10–2	14
Mozambique[2]	19°08′S, 33°08′E	EA	7–10	5
Zimbabwe[3]	17°49′S, 30°32′E	EA	10–2	9
FL, USA[4]	28°31′N, 81°23′W	EA	4–6	12
FL, USA[5]	28°30′N, 81°44′W	KA, BC	2–7	5
TX, USA[6]	30°09′N, 99°20′W	KA, BC		8
TX, USA[7]	30°09′N, 99°20′W	KA		16
Japan[8]	34°36′N, 136°6′E	EA, BC	6–8	7
IL, USA[9]	39°38′N, 89°28′W	EA, KA, BC, MR, DR	5–7	11
Canada[10]	45°04′N, 79°57′W	BC, MR	5–6	7+

Methods of validation are edge analysis (EA), mark recapture of chemically tagged fish (MRCT), length frequency (LF), back-calculation (BC), mark recapture (MR), known-age fish (KA) and counting of daily rings (DR). Period of opaque zone deposition given in months from 1 (January), to 12 (December).
[1]This study.
[2]Weyl and Hecht (1999).
[3]Beamish et al. (2005).
[4]Crawford et al. (1989).
[5]Hoyer et al. (1985).
[6]Howells et al. (1995).
[7]Buckmeier and Howells (2003).
[8]Yodo and Kimura (1996).
[9]Taubert and Tranquilli (1982).
[10]Maraldo and MacCrimmon (1979).

Edge Analysis indicated that the highest proportion of otoliths with opaque margins was obtained from fish sampled during early summer (November and January in South Africa). This was consistent with EA results from other studies (Table 4) and may be a result of a lag between zone deposition and detection. This is because the state of the growth zone formed at the edge of the otolith only becomes visually discernible after it is deposited. As a result, opaque margins detected in early summer had to have been deposited during a slow growth period sometime previously. Such a slow growth period is most likely linked to decreased metabolic rates during low winter temperatures (Lemons and Crawshaw, 1985) and energy costly spring spawning (Cooke et al., 2001). While the influence of each on growth zone deposition is unknown, it is likely that their combination is responsible for growth zone deposition in the otolith.

Annual growth zone deposition in *M. salmoides* sagittal otoliths found in this study was also consistent with findings from validation studies conducted through the present distributional range of this species in an array of climatic conditions ranging from 45°N to 33°S, as has been found by Maceina et al. (2007) in an assessment of the State and Provincial Fisheries Agencies and the ageing literature from North America and Canada. While growth zone deposition rate has not been validated for otoliths from tropical *M. salmoides* populations, Britton and Harper (2005) working on equatorial Lake Naivasha used marginal increment analysis and corroboration with length frequency data to validate the annual deposition of growth checks on scales. Since there is evidence that growth zone deposition rates are similar between scales and otoliths (Maraldo and MacCrimmon, 1979) annual growth zone deposition can be inferred. Our data therefore support the hypothesis that a single opaque/hyaline growth zone is deposited on *M. salmoides* otoliths throughout their distributional range and is in support of the assumptions made in non-validated ageing studies conducted on this species elsewhere (e.g. Godinho and Ferreira, 1993; Lorenzoni et al., 2002; Neal and Noble, 2002; Rodriguez-Sánchez et al., 2009). Future validation studies should concentrate on the more robust MRCT method, which is commonly used to identify the effect of fish stocking (Doe, 2005; Hoffman and Bettoli, 2005) but has not been previously used to validate growth zone deposition rate in *M. salmoides* (Table 4).

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